Kazuo SUZUKI*: Biosystematic studies of Japanese *Epimedium* (Berberidaceae) (2) Variation of the populations in Kyushu (Part 2)**

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E. grandiflorum: The five populations (6, 7, 18–20) indicated in Fig. 6 were referable to this species. They were characterized by long sepals (8–17 mm), long-spurred petals (11–22 mm), ternate leaves, a large number of serrations, acuminate leaflet apices and annual leaves. Three of the five populations occurred in the uplands of limestone regions, while two others were located in a grassland and in the edge of a sparse forest, respectively (Table 1).

As shown in Fig. 7, the five populations were considerably variable in the characters analyzed. The populations 6 and 18 were largely deviated in inner sepal length, the ratio of number of serrations/midvein length, and spur length, while the other populations showed intermediate features which connect the two extremes. Variations in these characters could be regarded as clinal (north-south), when the locations of the populations were taken into account. On the other hand, populations 7 and 20 were sharply contrast in hair density on the upper surface of leaves and petiole length of a stem-leaf (Fig. 7). A considerable interpopulational difference was also observed as regards the hair density on the lower surface of leaves (Fig. 7).

Herbarium specimens from Oguni, Takamori and Mt. Noke-eboshi and a living plant from Hagi in Kumamoto Pref. were referable to *E. grandiflorum.*

Several characters other than those described above were also examined. They were, however, not significant taxonomically at least as far as the populations in Kyushu were concerned. White flowers were predominant throughout the populations in Kyushu, while pale red-purple flowers were observed in a few individuals in the populations of *E. trifoliatobinatum* and *E. grandiflorum,* and some on the Maino population described below. The length and habit of

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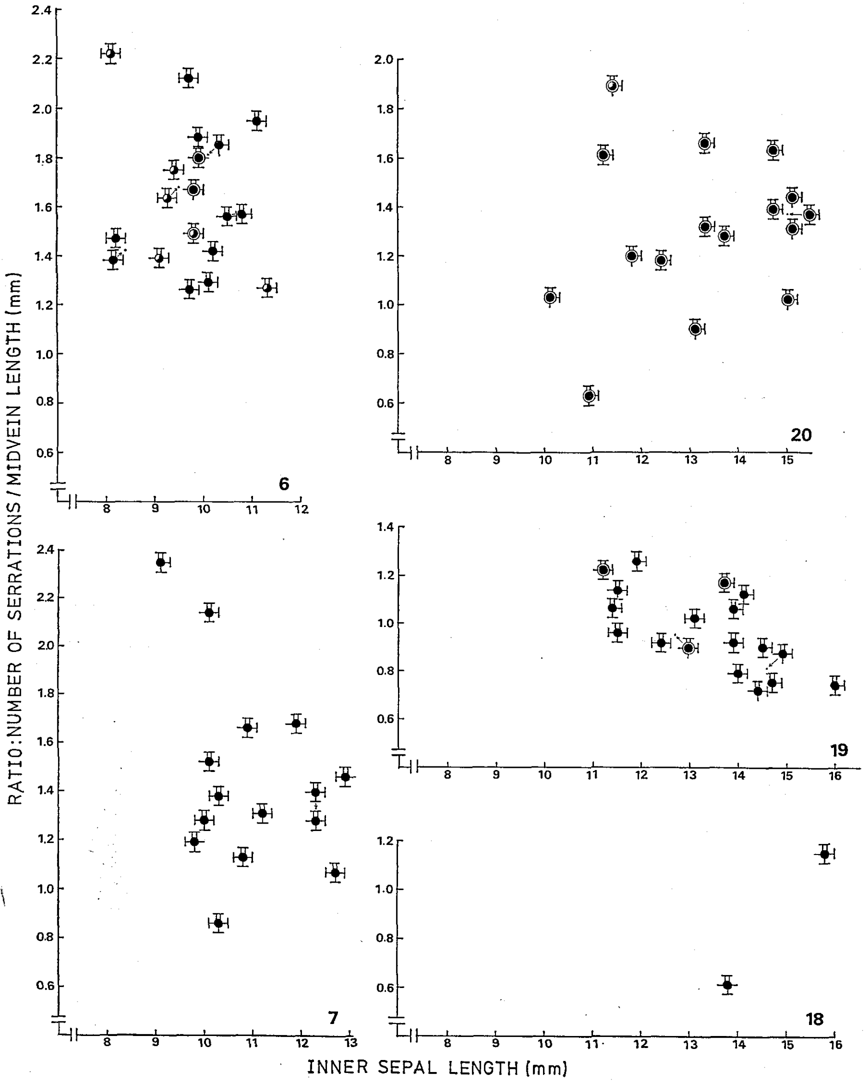

Fig. 6. Scatter diagrams showing the character correlation in the collections from five populations: 6, Senomoto-A; 7, Senomoto-B; 18, Sakaime; 19, Mizunashi; 20, Takenogawa—*E. grandiflorum*. Legends for symbols as in Table 2.

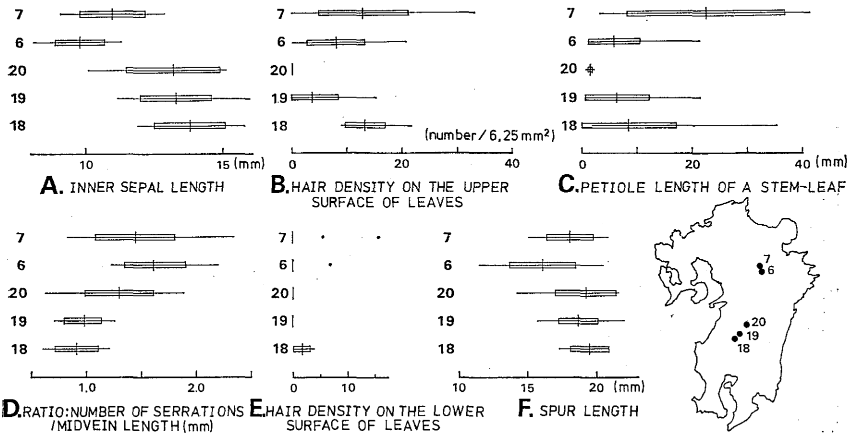

Fig. 7. Morphological variations in *E. grandiflorum*. Further explanation in text.

the hairs on the upper surface of leaves were variable among individuals even in a population.

Populations showing problematical variability and affinity. An unusually great variation was observed in two populations (9 and 13). These populations included the individuals which clearly deviate from typical form of the above three species in the combination of morphological characters or they are intermediate in some features. The individuals which can be identified as one of these species also grew in mixture.

Ukenokuchi (9 in Fig. 8) : In this population, four typical *E. grandiflorum* (indicated by arrows) and 21 aberrant types were observed. Most of the aberrant types showed a mixture of morphological features of *E. grandiflorum* and *E. trifoliatobinatum*. As examples, mention is given to the two collections accompanied by 1) and 2) in Fig. 8[1]. One of them with 1) had a short spur (T), C-type ramification (T), and hairless lower surface of leaves (G). Another example with 2) had a shorter spur (T), a-type leaflet apex (D), F-type ramification (G), and hairless lower surface of leaves (G). The other aberrant types had likewise the combinations of the features that could not be observed in members of the "pure" populations.

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1) The following abbreviations are used: G, a characteristic of *E. grandiflorum;* T, *E. trifoliatobinatum;* D, *E. diphyllum;* D-T, intermediate between D and T; T-G, intermediate between T and G.

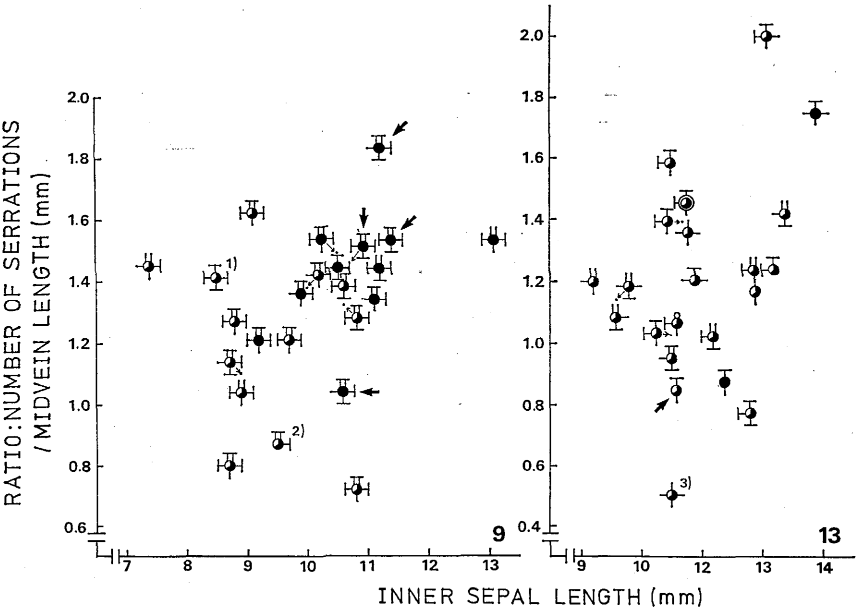

Fig. 8. Scatter diagrams showing the character correlation in the collections from two problematical populations: 9, Ukenokuchi; 13, Maino. Legends for symbols as in Table 2. Four arrows in 9 indicate typical *E. grandiflorum* and an arrow in 13 indicates typical *E. trifoliatobinatum*. See text as to the collections accompanied by the numerals 1)–3).

Maino (13 in Fig. 8) : In this population, an individual of *E. trifoliatobinatum* (indicated by an arrow) which was close to the Shikoku type mentioned above was observed. The other 21 individuals were aberrant types. One of the aberrant types accompanied by 3) in Fig. 8 was characterized by having a short spur (T), b-type leaflet apex (T), B-type ramification (D-T), and low hair density on the lower surface of leaves (T-G). The others were unusual in character expression as well.

Pollen fertility. Most individuals in every population showed over 80% in pollen fertility (Table 3), and aberrant individuals in problematical populations showed as high fertility as the individuals typical of the representative types.

Discussion From the results described above, it is clear that most of the populations in Kyushu have a minor intrapopulational variability, and these populations can be grouped into three species: *E. diphyllum*, *E. trifoliatobinatum* and *E. grandiflorum*. Though Shimizu (1960) and Kitamura & Murata (1961)

Table 3. Number of individuals showing respective pollen stainability

Locality	Pollen stainability (%)							
	30-40	40-50	50-60	60-70	70-80	80-90	90-100	undeterminable
1. Shijiki	0	1	0	0	2	2	10	0
2. Arie	0	0	0	0	0	1	24	0
3. Haruki-A	0	0	0	0	0	0	8	0
4. Haruki-B	0	0	0	0	0	0	20	0
5. Mt. Kora	0	0	0	0	0	0	9	0
6. Senomoto-A	0	0	0	1	0	0	17	2
7. Senomoto-B	0	0	1	0	0	2	13	1
8. Mt. Waita	0	0	0	0	0	2	15	1
9. Ukenokuchi	0	0	0	0	0	0	22	6
10. Kijima	1	0	0	0	1	4	16	0
11. Isl. Oshima	0	0	0	0	1	1	26	0
12. Isl. Shimanoura	0	0	2	1	0	1	25	1
13. Maino	0	0	0	3	0	0	21	0
14. Zaikoji	0	0	0	0	0	1	14	1
15. Kawaminami	0	0	0	0	0	1	20	0
16. Chishanoki	0	0	0	0	0	2	28	0
17. Ganjoji	0	1	0	0	0	0	25	0
18. Sakaime	0	0	0	0	0	2	4	0
19. Mizunashi	0	0	0	0	1	0	17	2
20. Takenogawa	4(1*)	6	0	1	1	0	3	0

* less than 30%

recorded *E. kitamuranum* from Kyushu, my observations did not confirm the occurrence of this plant in Kyushu. Populations at Ukenokuchi and Maino, which showed unusual intrapopulational variability, may have been brought forth in connection with interspecific hybridization considering the character associations of the aberrant types (cf. Suzuki, 1978). High pollen fertility of the aberrant individuals suggests that no restriction of gene exchanges among members of a population, including hybrid derivatives, would have occurred.

The present work has uncovered that different trends in evolutionary divergence can be discerned among the three species designated above. In *E. diphyllum*, the northern (1-5, 8, 10) and the southern (14-17) populations are somewhat different in structure. As is clear in Fig. 4, the southern populations are uniform and are composed of the individuals closely related one another. They can be regarded to represent the "pure" population of *E. diphyllum.*

On the other hand, the northern populations are more variable intrapopulationally. Individuals with a high rate of the number of serrations/midvein length of a leaflet, the almost acute leaflet apex or the C-type ramification are not rare in these populations. Because the three characteristics mentioned above commonly occur in typical forms of *E. kitamuranum* and *E. trifoliatobinatum* (cf. Figs. 6 and 7 in Suzuki, 1978), it is assumed that the northern populations of *E. diphyllum* in question would have been affected by introgression from either or both of these two species. If *E. kitamuranum* and *E. trifoliatobinatum* themselves could be regarded to be derived from introgressive hybridization between *E. diphyllum* and *E. grandiflorum* (Suzuki, 1978), the ultimate donor of the genes which have caused deviated character expressions in members of the *E. diphyllum* populations in northern Kyushu would be *E. grandiflorum*. Although the exact donor plant could not be demonstrated at present, it seems doubtless that the differentiation of the populations of *E. diphyllum* is connected with introgression from the other species.

E. trifoliatobinatum in Kyushu has slightly less serrations on leaves and somewhat broader leaflets than that in Shikoku. Populations in Kyushu have been found only at maritime areas and are characterized by bienniality and hardening of leaves. A similar type has also been observed in the southwestern part of Shikoku (Suzuki, 1978). Most of the populations in Shikoku are, however, confined to the interior serpentine regions and scarcely show bienniality and hardening (Suzuki, 1978). The Kyushu type of *E. trifoliatobinatum* may most probably represent a race that has been brought about by adaptation to maritime environments, as exemplified in *Layia* and *Achillea* (Clausen et al.; 1947, 1948). The infraspecific differentiation observed in this species is therefore not only geographical but also ecological.

E. grandiflorum is characterized by greater interpopulational polymorphism than *E. diphyllum* and *E. trifoliatobinatum*. As shown in Fig. 7, the six characters analyzed in *E. grandiflorum* of Kyushu considerably vary among the populations, though degrees of variability of these characters are unequal. The correlations between the characters are not always obvious. This situation seems to be related with the fact that *E. grandiflorum* usually grows in isolated and closed habitats. Populations 18–20 were found on limestone cliffs, and populations 6 and 7 were located in small patches of a grassland and the edge of a sparse forest in the uplands respectively. It seems plausible that, when compared with the other species of *Epimedium*, gene flows between populations may have been more limited in *E. grandiflorum* and the effects of selection and genetic drift would have been greater for making up the present population composition of this species. In this respect, the situation of *E. grandiflorum* in this area is similar to those of *Agrostis tenuis* (Bradshow, 1959), *Eschscholzia californica* (Cook, 1962) and *Collinsia heterophylla* (Weil et al., 1964).

Mention should be given to the following two observations. First, the presence of persistent hairs on the upper surface of leaves, which Shimizu (1960) recognized as a diagnostic character of *E. grandiflorum* var. *higoense*, is variable among individuals within a population according to the present analysis and may not be a good taxonomic character. Second, though *E. grandiflorum* in Shikoku could be divided into two groups on the basis of petiole length of a stem-leaf (Suzuki, 1978), the same is not true of the populations in Kyushu since the petioles greatly vary from long to short types within a population in the latter (Fig. 7, C).

The present work strengthens the belief that factors contributing to the enormous complexity of *Epimedium* in Japan are manifold. Though the work development of reproductive isolation between species seems to be the utmost importance among the factors that have caused this complexity, other factors, such as ecological differentiation and genetic drift in connection with geographical separation, are apparently involved. Experimental studies in elucidating the significance of some of these factors are now in progress and will be reported in a subsequent paper.

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九州産イカリソウ属 (*Epimedium*) 植物の20集団からサンプリングを行い，形態的変異及び花粉の稔性について調べた。その結果，九州ではバイカイカリソウ (*E. diphyllum*)，ヒメイカリソウ (*E. trifoliatobinatum*)，イカリソウ (*E. grandiflorum*) の3種が認められ，それぞれの種に特異的な変異性が見られた。九州南部のバイカイカリソウ集団が比較的均一であるのに対し，北部の集団ではより変異に富んでいる。この変異性は浸透性交雑によるものと思われる。九州産のヒメイカリソウ集団は四国の蛇紋岩地で見られたものとは幾分異なり，海岸適応と思われる型に生態的にも分化している。イカリソウでは地理的多型性が見られた。これは閉鎖的な環境下における集団間隔離機構の発達により，自然選択と遺伝的浮動が強く働いたためと思われる。一方，これらの集団とは別に，変異の激しい2集団が見られた。これらの集団は上記種間の交雑起源と思われる。